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A REVISION OF THE REDFIELDIIFORM AND PERLEIDIFORM FISHES FROM THE TRIASSIC OF BEKKER'S KRAAL (SOUTH AFRICA) AND BROOKVALE (NEW SOUTH WALES)

BY

PETER HUTCHINSON
Drayton, Berks., England

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A REVISION OF THE REDFIELDIIFORM AND PERLEIDIFORM FISHES FROM THE TRIASSIC OF BEKKER'S KRAAL (SOUTH AFRICA) AND BROOKVALE (NEW SOUTH WALES)

By PETER HUTCHINSON

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SYNOPSIS

All the genera included in the Redfieldiiformes and Perleidiformes (Chondrostei) from the Triassic localities at Bekker's Kraal (South Africa) and Brookvale (New South Wales) are redescribed. In addition, *Ischnolepis*, an early redfieldiiform from Zambia is redescribed. The order Redfieldiiformes is divided into three families; the Brookvaliidae, the Redfieldiidae and the Schizurichthyidae nov. The order Perleidiformes is divided into four families; the Aetheodontidae, the Colobodontidae, the Cleithrolepididae and the Hydropessidae, a new family erected for the inclusion of *Hydropessum*, a genus previously thought to be a cleithrolepid. A functional analysis is made of the redfieldiiform skull and it is concluded that the Redfieldiidae possessed a unique suctorial feeding mechanism. Growth and development of the tail in *Brookvalia gracilis* is described, and the palaeoniscoid body lobe squamation is discussed. It is concluded that reversal of body lobe scale rows does not occur in palaeoniscoids.

I. INTRODUCTION

Triassic fish from Bekker's Kraal were first described by Broom (1909) and subsequently by Brough (1931, 1934) while those from Brookvale, N.S.W. were described by Wade (1935). It is clear from more recent publications on Triassic fish that comparative studies have been limited by the incomplete nature of these earlier descriptions (see, for example, Schaeffer 1955 : text-figs 7 and 8; 1967 : text-figs 17 and 18), and a redescription of the Redfieldiiformes and Perleidiformes from Brookvale and Bekker's Kraal has been attempted to remedy this. In addition it was clear that a redescription of *Ischnolepis* from Zambia (Haughton 1934) would help in an attempt to understand the early redfieldiids.

With the exception of *Ischnolepis*, the specimens described here required no preparation. The Brookvale specimens are impressions and natural casts of fish which have been crushed to a thickness of at most a few millimetres. The Bekker's Kraal fossils are, in the main, impressions, although replacement minerals are sometimes present.

Of the material studied here, only *Ischnolepis* was preserved in a relatively uncrushed state. Specimens of this genus were preserved in a matrix of acid resistant, fine grained mudstone, and I have been able to remove this matrix with an ultrasonic probe, revealing many new features. The ages of the three localities will now be discussed briefly:

Zambia. The locality of the type material of *Ischnolepis bancrofti* is the Lunsempfwa valley, Zambia (lower part), and is described as 'probably Upper Beaufort or Lower Stormberg' (Haughton 1934 : 97). However, specimens of *I. bancrofti* in the British Museum (Natural History) are registered as coming from the Madumabisa shales, 82 miles from Kabwe (Broken Hill), and north of the junction between Tutenge and Lunsempfwa rivers, at latitude 14°43′ south, and longitude 29°38′ east. The Madumabisa mudstones and shales are generally thought to extend from Ecca formation times to the Cistecephalus zone, therefore not extending beyond the uppermost Permian (Gair, 1960 : 9; Drysdall & Kitching, 1963 : 34). It has been suggested, however, that plant remains from the uppermost parts of the Madumabisa mudstone in Rhodesia indicate that these beds in fact extend to the top of the Beaufort Series, and that they include a condensed succession which is equivalent to the Lystrosaurus and Cynognathus zones (Bond 1965). This extension of the possible upper limits of the Madumabisa mudstones to include the Lower Triassic epoch means that, unless the locality of *I. bancrofti* is more exactly identified, its probable age can only be defined as uppermost Permian or Scythian.

Bekker's Kraal. The Bekker's Kraal fish are found in a sandstone layer 20 mm thick which occurs in a 10 metre thick bed of sandstone which, in turn, forms part of the lower Cynognathus zone succession in Orange Free State (Watson 1931). They are therefore Scythian in age—Upper Scythian according to Romer (1947) or Lower Scythian according to Cosgriff (1969).

Gosford, Brookvale and St. Peters. These three Australian localities occur in the Sydney basin where the Triassic is divided into three groups: Narrabeen, Hawkesbury and Wianamatta. These are subdivided as follows (youngest at top):

WIANAMATTA	Camden Subgroup	
	Liverpool Subgroup (including the Ashfield shale)	ST. PETERS FAUNA
HAWKESBURY	Hawkesbury sandstone	BROOKVALE FAUNA

NARRABEEN	Gosford formation	GOSFORD FAUNA
	Collaroy claystone	
	Tuggerah formation	
	Munmorah conglomerate	

(Banks *et al.* 1969)

The Munmorah conglomerate overlies the Newcastle Coal Measures, the uppermost coal seam of which traditionally marks the upper limit of the Permian. However, the validity of this boundary has been questioned by several authors because various coal seams appear to have been regarded as being the uppermost in various localities. The Permo-Triassic contact may in fact be 'an undulating surface with marked relief' (Balme 1969 : 108). Moreover, the lower part of the Munmorah conglomerate contains a Permian flora including *Glossopteris*, *Schizoneura*, *Phyllotheca* and *Cladophlebis*, while the upper part contains the first record of the spore *Aratrisporites*, which is characteristic of Lower Triassic strata in many parts of the world (Helby 1966). The true Permo-Triassic contact probably therefore lies within the Munmorah conglomerate.

Above the Munmorah conglomerate there are about 2000 feet of shales and sandstone (Wade 1941b) which, if the age of the Permo-Triassic boundary given above is correct, may be regarded as representing the Scythian. Obviously, with no further information, it is not possible to say whether these sediments represent part or all of the Scythian, or even whether they extend into the Anisian. The Gosford fish fauna, which is found in the uppermost of these beds, is therefore very tentatively placed at the Scythian/Anisian boundary.

There are 550 feet of sandstones (the lower part of the Hawkesbury sandstone) between the Gosford and Brookvale horizons (Wade 1935), but within these sediments there are signs of an erosional hiatus, and incomplete palynological data indicate that this may represent a substantial time break (Helby, pers. comm). The Brookvale fauna may therefore be considerably younger than that of Gosford, and is here tentatively regarded as being Ladinian in age.

II. SYSTEMATIC DESCRIPTIONS

Order REDFIELDIIFORMES

Diagnosis. Small to moderately large fusiform chondrostean fishes. Skull bones usually ornamented with ridges or tubercles. Skull roof composed of extrascapulars, parietals, dermosphenotic, frontals and dermopterotic. Extrascapulars and parietals sometimes divided. Dermopterotic deep, dermosphenotic either rectangular or crescent-shaped. A postrostral may or may not be present. Snout composed of nasals, antorbitals and rostral, and sometimes adnasals and premaxillae. A single nostril present. Nasals small, bordering dorsal edge of nostril. Antorbital bordering anterior edge of orbit and ventral edge of nostril and, in forms which lack premaxillae, the ventral edge of the snout. Opercular series oblique to vertical, composed of opercular, subopercular and one, or rarely two, plate-like branchiostegals. Preopercular high and 'r'-shaped. Maxilla expanded posteriorly and attached to cheek. Teeth conical and pointed. Braincase of palaeoniscoid type.

Scales rhombic to leaf-shaped or, in the Schizurichthyidae, rectangular to subcircular with peg and socket articulation; dentine layer absent. Dorsal and anal fin-rays more numerous than endoskeletal supports, jointed and bifurcated; leading rays usually bearing fringing fulcra. Jointing and fringing fulcra often reduced in paired fin-rays. Caudal fin with abbreviated body lobe.

Family **BROOKVALIIDAE** Berg 1940

Diagnosis. Orbit large. Two pairs of parietals (except in *Atopocephala*). Dermopterotic deeper than dermosphenotic. Posterior extension of supraorbital sensory canal, if present, on dermopterotic. Dermosphenotic narrow and crescent-shaped, tapering to a point anteriorly. Frontal curved, and running close to, or actually touching, orbital edge. Snout composed of rostral, and paired antorbitals, nasals and premaxillae. Postrostral present in some genera, probably lost in *Atopocephala*. Antorbital a narrow curved element, bordering the anterior edge of the orbit, with a narrow anterior extension bordering the ventral edge of the nostril. Antorbital separated from the ventral edge of snout by premaxilla. Adnasal absent, or, if present, small and diamond-shaped, having no contact or point contact with dermosphenotic. A single dermohyal present. An antopercular present. Infraorbital elements either separating maxilla from orbital edge or reduced so that maxilla actually borders orbital edge for a short distance. Gular plate present. Lower jaw slender, long and curved dorsally towards the symphysis. Elements of pectoral girdle generally narrow. Fulcra on dorsal and anal fins small or absent. Scales rhomboidal to leaf-shaped. Hinge line at base of body lobe not usually marked by abrupt change in orientation of scales.

Genus ***ISCHNOLEPIS*** Haughton 1934

1934 *Ischnolepis* Haughton: 97.

Diagnosis (emended). Head bullet-shaped with an extremely large orbit anteriorly placed. Skull bones ornamented with small tubercles. Two pairs of parietals, posterior element triangular, though smaller than in *Brookvalia*. Dermopterotic rectangular. No extension of the supraorbital sensory canal on dermopterotic. Frontal extending anteriorly just beyond the level of the midpoint of the orbit. Opercular series longer than in *Brookvalia*, and moderately oblique. Preopercular with an antero-ventral extension running for a short distance above the antero-dorsal edge of the maxilla. Infraorbital elements very narrow. Teeth slightly recurved.

Body fusiform. Pectoral girdle ornamented with parallel ridges. Scales leaf-shaped, each ornamented with a row of tubercles. Jointing regular on all fin-rays except on those of the pectoral fin. Anal fin opposite the dorsal fin, with an extended base and long anterior rays. Caudal fin hemiheterocercal.

TYPE (and only) SPECIES. *Ischnolepis bancrofti* Haughton.

REMARKS. *Ischnolepis* is probably the earliest known redfieldiiform genus. This new description was made possible only after preparation of specimens in the British Museum (Natural History) using an ultrasonic probe—a remarkably sensitive tool in certain circumstances (Macadie 1967).

Ischnolepis is similar to members of many palaeonisciform families, but it already displays characters which are diagnostic of the family Brookvaliidae, such as a narrow crescent-shaped dermosphenotic and an opercular series which includes a single branchiostegal ray.

Ischnolepis bancrofti Haughton

(Figs 1–6)

1934 *Ischnolepis bancrofti* Haughton: 97–101, text-figs 1–2, pl. 29.

HORIZON AND LOCALITY. Upper Permian or Scythian. Madumabisa shales, 82 miles from Kabwe (Broken Hill), Lunsempfwa Valley, Zambia.

DIAGNOSIS. As for the genus *Ischnolepis*.

HOLOTYPE. S.A.M. 9338 with counterpart S.A.M. 9339.

MATERIAL. Photographs of holotype, P.27577–9.

The material in the B.M.(N.H.) consists of two blocks (part and counterpart; P.27577–8) and several fragments (collectively P.27579); all contain specimens of *Ischnolepis* together with an unidentified palaeoniscoid.

DESCRIPTION. *Size* (Fig. 1). The total length from snout tip to the posterior end of the caudal fin in the most complete specimen is 62 mm. The body is fusiform.

Skull (Fig. 2). The overall shape of the skull is very similar to that of *Brookvalia;* it is bullet-shaped and its main features are a large orbit, a moderately oblique opercular series and a slender, curved lower jaw. Almost all the skull bones are ornamented with rugae.

The suprascapular is ornamented with a few tubercles and with elongate rugae which radiate from its antero-dorsal corner. In a specimen on block P.27578, the inner surface of the dermopterotic bears a ventral lamina which runs close to the ventral border of the bone. The posterior end of this lamina appears to be in close association with the dorsal tip of the ascending process of the parasphenoid.

Dorsal to the dermopterotic there are two parietals, the posterior of which is triangular and small, and usually poorly preserved. The anterior extent of the anterior parietal is marked only by a ridge seen in a specimen on block P.27577 (Fig. 3). There is no sign of any extension of the supraorbital canal onto the parietal. The anterior end of the dermosphenotic is very narrow and appears to converge to a point, although its extreme tip is not preserved. Its ventral border is ornamented with four ridges which consist of rows of closely associated rugae. The relationship between the dermosphenotic and the postorbital and suborbital bones is not clear (Fig. 3), the skull roof, including the dermosphenotic, being displaced relative to the cheek bones. In my restoration (Fig. 2) the dermosphenotic has been

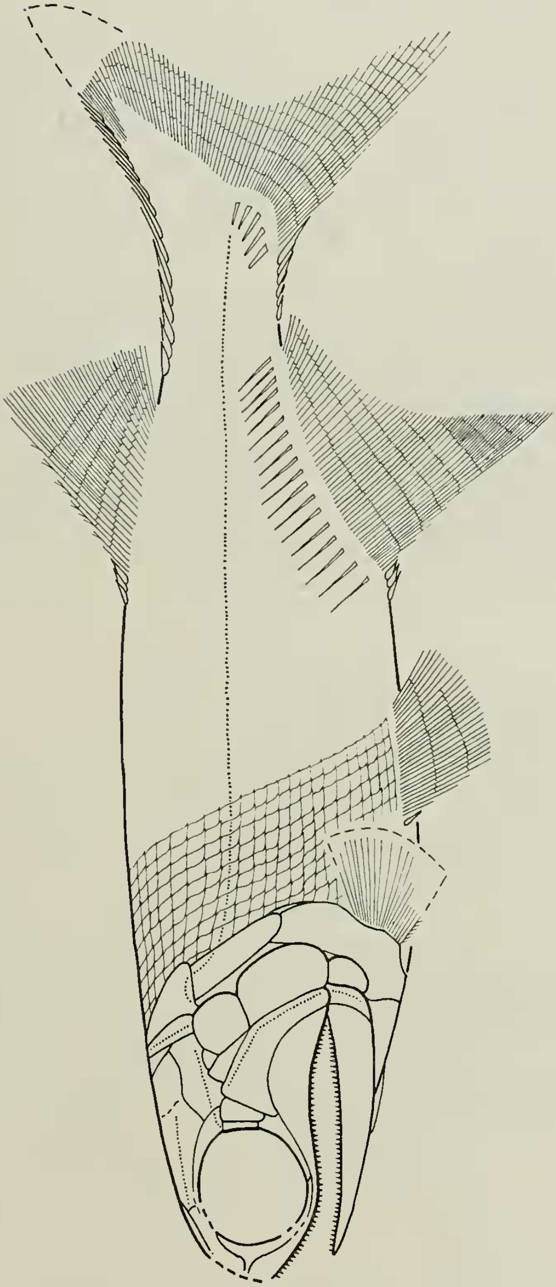

FIG. 1. *Ischnolepis bancrofti* Haughton. Restoration, ×2·5 approx. Posterior scales omitted.

drawn so that its ventral edge continues the curve of the orbit border suggested by the anterior margin of the postorbital.

There is only one branchiostegal. Several specimens were prepared to reveal the ventral side of the pectoral girdle and the lower jaws. During this preparation, delicate bones of the gill arch system were revealed, and if branchiostegals had been present it is likely that they would have been seen. Schaeffer's opinion (1967 : 334) that *Ischnolepis* lacks a complete branchiostegal series is thus confirmed. Haughton (1934 : 99) observed branchiostegals in *Ischnolepis*, but only in a single fragment; in this context it is significant that mixed with the specimens of *Ischnolepis* there are specimens of a palaeoniscoid, of similar size and proportions, which have eight pairs of branchiostegal rays.

The anterior edge of the subopercular lies at 65° to the ventral margin of the maxilla; the orientation of the opercular series is thus almost identical to that of *Brookvalia*. The ornament on the subopercular varies from small tubercles to elongate rugae which radiate from a point about a third of the way down the anterior edge. As well as rugae, the subopercular bears faint concentric ridges which run parallel with its posterior border; these are probably the result of uneven growth.

In a specimen on block P.27578, and less clearly in one on block P.27577, there is a single plate-like diamond-shaped bone, which lies ventral to the lower jaw ramus.

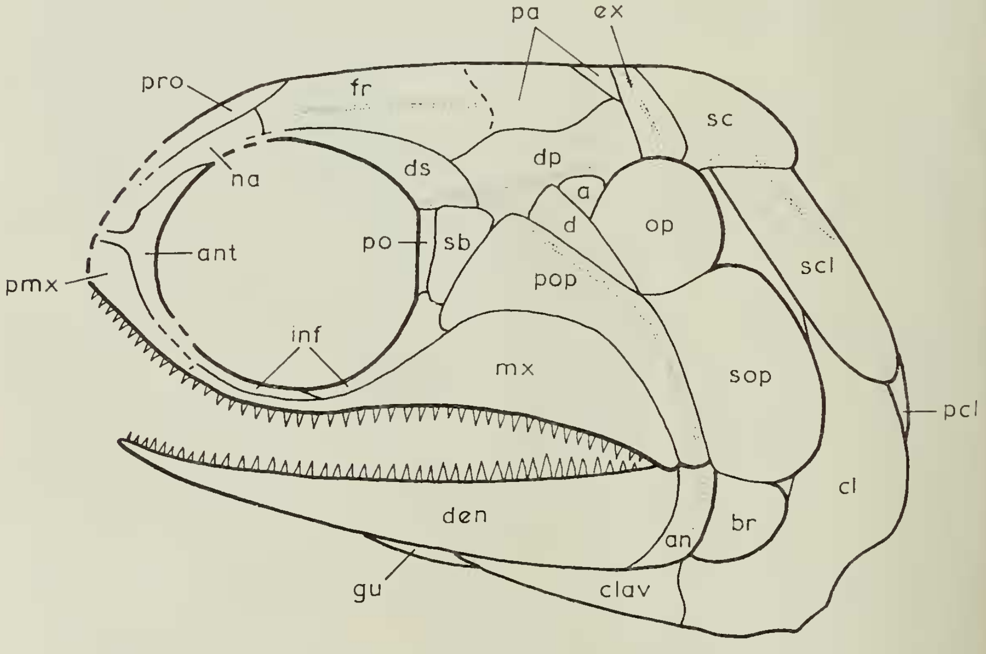

FIG. 2. *Ischnolepis bancrofti* Haughton. Restoration of skull and pectoral girdle, ×5·5 approx.

There are faint traces of grooves running parallel to its anterior margins. Although damaged, this bone appears to have been bilaterally symmetrical, and is therefore a mid-line element; probably a median gular.

In a specimen on block P.27577, a fragment of the right dermohyal is fused, or at least is in close contact, with the underlying hyomandibular. There is a tiny element lying ventral to the dermohyal, inserted between the antero-dorsal corner of the subopercular and the posterior margin of the preopercular. This element corresponds with the accessory opercular recorded in many palaeoniscoids (e.g. *Watsonichthys*, Gardiner 1963). It is seen only on the medial surface of the cheek (Fig. 3), laterally it is covered by the antero-dorsal corner of the opercular.

The preopercular has similar proportions to that of *Brookvalia*, except that its anterior limb extends antero-ventrally for a short distance dorsal to the antero-dorsal border of the maxilla. Along the posterior part of the suture between the preopercular and the maxilla there is a very shallow medial lamina on the preopercular which underlaps the maxilla (Fig. 3). Further anteriorly there is a groove in the antero-dorsal edge of the maxilla which receives the antero-ventral part of the preopercular. Ornament on the maxilla consists of tubercles and some elongate rugae which radiate from the point on its ventral margin which lies below the posterior edge of the orbit. The posterior infraorbital is expanded posteriorly and has a complex postero-dorsal edge: it butts against the postorbital and the antero-ventral tip of the preopercular and, between these two contacts, is notched to receive

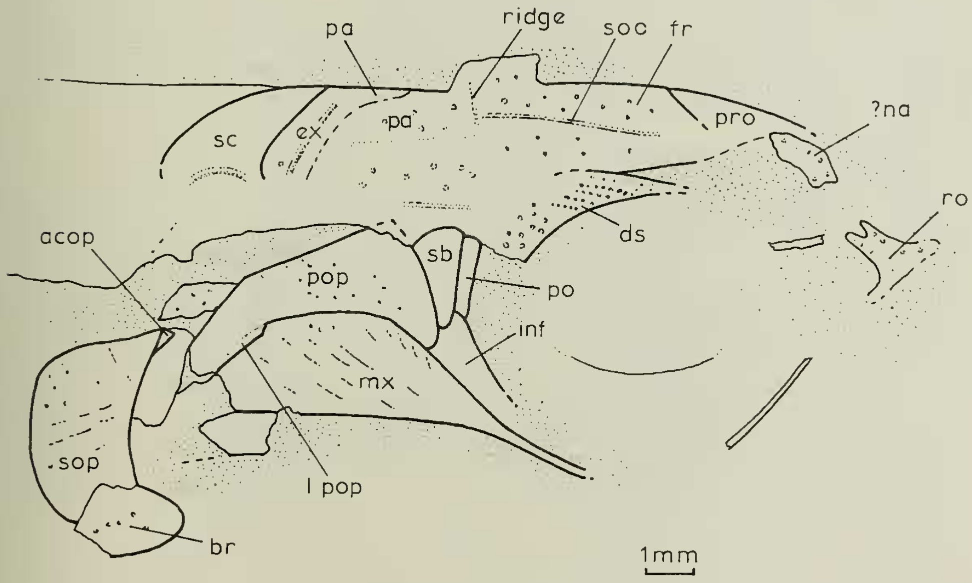

FIG. 3. *Ischnolepis bancrofti* Haughton. P.27577: cheek, left side internal view; roof, impression of left side.

the ventral tip of the suborbital. The anterior infraorbital extends along the ventral border of the orbit and is extremely narrow and, as at this same point the maxilla is narrow, the infraorbital bar is very slender.

The snout is poorly preserved. In a specimen on block P.27578, there is a fragment of bone sutured to the anterior end of the left frontal which is probably part of the nasal. A narrow curved fragment seen in a specimen on block P.27577 (Fig. 3) is probably also nasal. Neither of these fragments gives any indication of the anterior extent of this bone. A postrostral is preserved in the specimen noted above (on P.27578). It is lozenge-shaped, smooth and has a peg-like extension at its anterior end. A poorly preserved rostral (on P.27577, Fig. 3) bears a notch which probably accommodated this peg.

There is clear evidence of only one other bone in the snout region. This is a narrow curved antorbital which borders the anterior margin of the orbit. Midway along its anterior edge there is an anterior process. It is not certain whether a premaxilla is present, although in a specimen on block P.27577, an elongate tooth-bearing element is seen lying medial to the anterior end of the right maxilla. Anteriorly this element is expanded and it is thus unlikely to be entirely composed of maxilla. Comparison with *Brookvalia* suggests that it is premaxilla, but the possibility that it is partly rostral or a rostro-premaxilla must be admitted.

Lower Jaw (Fig. 4). The lower jaw is deep posteriorly and tapers towards the symphysis so that the anterior part is very slender. The dentary is a thin lamina of bone ornamented with elongate rugae. It bears conical teeth which are 0·5 mm high. Halfway up each tooth there is a slight constriction above which the profile is somewhat bulbous. In lateral view the profile is asymmetrical, the tip being slightly recurved (Fig. 4). In a specimen on block P.27578, broken teeth show that the outer enamel layer is about 0·03 mm thick. Only posterior teeth are preserved. They are closely spaced, and it is estimated that there were as many as 50 on the dentary.

The meckelian bone extends along the entire length of the medial side of the lower jaw. Anteriorly, where it is best preserved, it has a round cross-section. There is a narrow element, also round in cross-section, running immediately below the meckelian bone. Comparison with *Pteronisculus* (Nielsen 1942) suggests that, for most of its length at least, this is part of the dentary and consists of a tube enclosing the mandibular canal. In *Ischnolepis* this structure is only 0·3 mm deep in side view and it was not possible to ascertain whether or not it contained a canal. Above the meckelian bone there is an indeterminate number of coronoid elements. It is not known to what extent these thin bones overlapped the meckelian bone on its medial side. The internal edges of the internal lamina of each coronoid bear low conical teeth which are about 0·15 mm high. It is estimated that there were originally about 50 of these teeth along the length of the lower jaw. In addition, 9 small teeth are situated on the posterior coronoid (or the posterior part of the posterior coronoid) which slopes postero-dorsally close to the jaw articulation. Numerous extremely small teeth are scattered on the surface of the internal lamina of the coronoids.

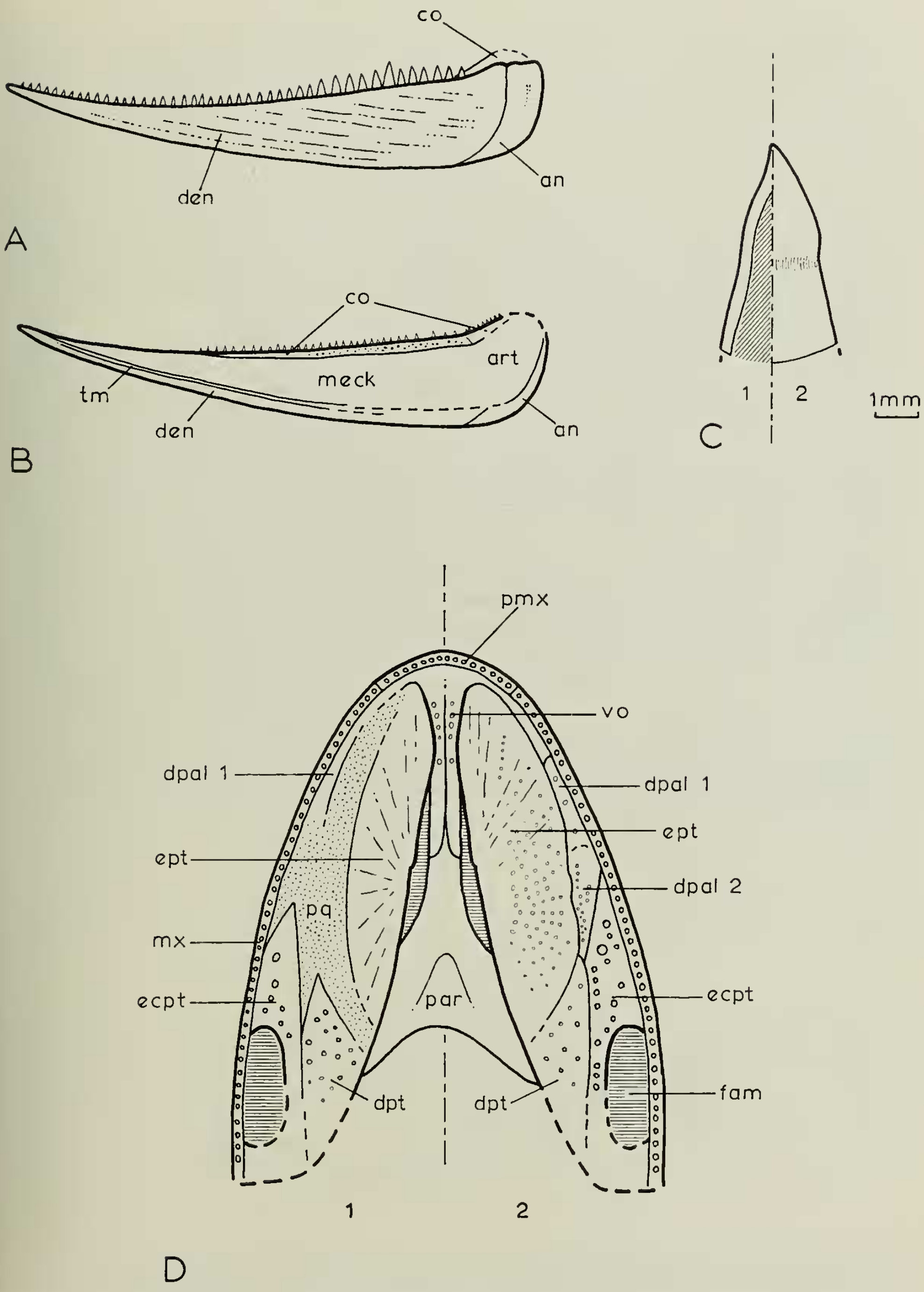

Fig. 4. *Ischnolepis bancrofti* Haughton. (A) Lower jaw. Restoration of right ramus in lateral view, coronoid teeth omitted, ×5·5 approx. (B) Lower jaw. Restoration of left ramus in medial view, dentary teeth omitted, ×5·5 approx. (C) Dentary tooth from P.27578: 1, in section; 2, in lateral view. (D) Restoration of palate in ventral view, ×5·5 approx.; 1, incompletely ossified; 2, completely ossified.

Palate. The palatoquadrate complex is preserved in several specimens. In one (on block P.27577) growth of the dermal bones associated with the palatoquadrate is incomplete, whereas in others the palate has a complete covering of dermal bones (Fig. 4). The dermal bones associated with the palatoquadrate have been restored in ventral view (Fig. 4). The endopterygoid is the main anterior element. Its centre of ossification lies almost halfway along the medial border of the palatoquadrate. Rows of tiny teeth radiate from this centre of ossification. An unusual feature of the palate is that the endopterygoid is completely separated from the ectopterygoid by a junction of the posterior dermopalatine and the dermometapterygoid. The dermometapterygoid is comparable in size with the endopterygoid, and forms the major part of the postero-dorsal surface of the palate.

The lateral edge of the endopterygoid is bounded by two dermopalatine elements, the anterior of which is narrow and bears a single row of teeth. The posterior dermopalatine is slightly broader and bears three rows of small teeth running parallel to the long axis of the bone. Posterior to the dermopalatines there is a broad ectopterygoid, which extends posteriorly as a narrow strip running alongside the lateral border of the dermometapterygoid. The ectopterygoid bears several rows of teeth, those in the centre row being comparable in size with those of the dentary.

The toothless parasphenoid extends between the anterior part of the palatoquadrates, but its relationship with the snout is unknown. Posteriorly it bifurcates so that its overall shape corresponds to an inverted Y. The major part of the posterior half of the parasphenoid consists of the two ascending processes. These are narrow and elongate and appear to extend to the lateral walls of the skull for, in a specimen on block P.27578, the distal end of the left ascending process appears to meet the posterior part of an internal lamina running along the inside of the dermopterotic, implying that a spiracular canal was present, as in *Pteronisculus*. The basipterygoid process is much smaller than the ascending process and is composed of a ventral fold of the lateral edge of the parasphenoid. There is an oval dome on

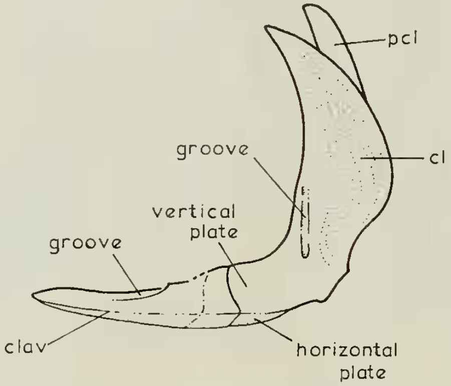

FIG. 5. *Ischnolepis bancrofti* Haughton. Restoration of dermal bones of left pectoral girdle, ×4·5 approx. Ornament on cleithrum restored from internal surface.

the ventral side of the centre of the posterior part of the parasphenoid. The function of this dome is unknown. Its position corresponds with that of a depression seen on the dorsal side of the parasphenoid in *Pteronisculus* (Nielsen 1942).

There are two narrow vomers ventral to the lateral edges of the anterior part of the parasphenoid. In a specimen on block P.27578 a short midline suture is seen at the anterior end of the parasphenoid, which suggests that the vomers met one another, at least anteriorly. The vomers, unlike the parasphenoid, bear small teeth.

Pectoral girdle. The ventral part of the pectoral girdle is restored in lateral view in Fig. 5. The supracleithrum is almost as wide as the ventral part of the suprascapular against which it butts. Ornament on the medial surface of the supracleithrum consists of grooves which run parallel to the long axis of the bone; a row of tiny tubercles runs along the bottom of each of these grooves. These are evenly spaced and number about 30 per mm. Only the postero-dorsal corner of the supracleithrum has a smooth surface.

The cleithrum bears a shallow groove on its lateral surface. Its medial surface is ornamented with very fine grooves which bear rows of tiny tubercles similar to those described on the inner surface of the supracleithrum. The anterior margin is devoid of any ornament.

The clavicle is narrow in lateral view, tapering to a point anteriorly; posteriorly it forms a broad lamina which overlaps the anterior end of the vertical plate of the cleithrum. Between this posterior lamina and the anterior half of the clavicle there is a groove which opens anteriorly, and extends posteriorly on the medial side of the posterior lamina. The clavicles appear to have met one another along almost their entire length.

Fins. The fins of *Ischnolepis* are well preserved, and a fairly complete account of their structure can be given. This description differs from that of Haughton (1934 : 97) mainly in that fringing fulcra are described only on the anterior rays of the pectoral fin, and less certainly on the dorsal fin. Several other fins with fringing fulcra are preserved in specimens P.27577 and P.27578, but these are associated with body fragments which cannot be assigned to *Ischnolepis* with certainty. As there is at least one other palaeoniscoid preserved with *Ischnolepis*, confusion could easily result from a description of any material with uncertain affinities, and information from doubtful specimens has not been used here.

Paired fins. The pectoral fin has 20 rays. The anterior ray has a base considerably broader than those of its fellows and bears fringing fulcra. Neither jointing, nor distal bifurcation was observed in any ray. The five anterior rays are associated with a single distal radial, and the two following rays with a second. The proximal ends of the other rays are not seen. The preservation of the pectoral fin in a specimen on block P.27577 suggests very strongly that its base, and therefore also the margo radialis, was orientated vertically.

The pelvic fin has a long base, so it is almost rectangular in shape. There are 29 rays which have 2 joints.

Unpaired fins. The anal fin is very large. Its base is 20% of the total body length. There are 51 rays, and as the anterior rays are six to seven times as long as the

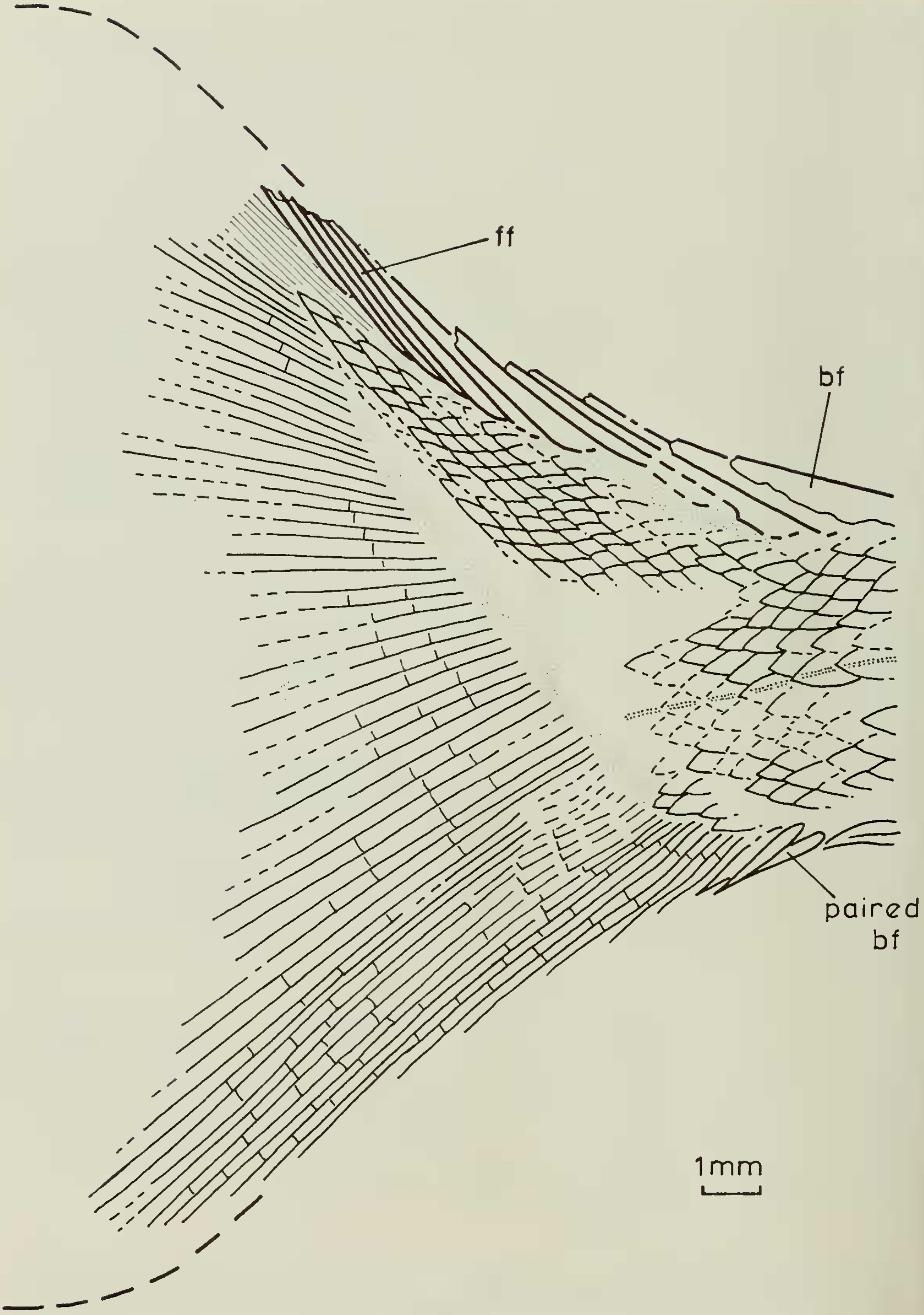

Fig. 6. *Ischnolepis bancrofti* Haughton. Caudal fin, P.27577. Right side.

posterior rays, the fin has an overall triangular appearance. The anterior rays have 8 joints and bifurcate distally, the posterior rays have as few as 2 joints and do not bifurcate.

The dorsal fin has 26 rays which have 5 joints, and which are bifurcated along almost their entire length. In some specimens there are faint traces of fringing fulcra on one of the anterior rays.

The caudal fin is well preserved except for the tip of the dorsal lobe (specimen in block P.27577, Fig. 6). Photographs of the holotype (S.A.M.9338) show that the lobes are equal in size and that the fin is not deeply cleft. The body lobe is long, extending over halfway along the length of the dorsal lobe. There are 66 rays; those of the dorsal lobe have 3 joints, and those of the ventral lobe up to 11 joints. The 7 anterior rays of the dorsal lobe are epaxial in position. Distal bifurcation was not observed in the specimens available for study, although this has been noted in the holotype (Haughton 1934 : 101).

Squamation. The scales are leaf-shaped, the largest flank scales being 0·8 mm long and 0·7 mm deep. They bear an ornament consisting of a row of closely spaced tubercles which form a ridge running postero-ventrally across each scale. There are 50 body transverse scale rows, containing about 30 scales in the region of the dorsal fin. The change in orientation of scales from body to body lobe is achieved gradually, so that there is no hinge line visible at the base of the body lobe.

Genus ***ATOPOCEPHALA*** Brough 1934

1934 *Atopocephala* Brough: 564.

Diagnosis (emended). Head bluntly pointed. Skull bones ornamented with tubercles. One pair of parietals. Dermopterotic short and deep. Frontal elongate, separated from the orbit edge by dermosphenotic. Snout region poorly known, but appearing to be similar to that of *Brookvalia.* Opercular series almost vertical. Opercular and subopercular of almost equal size, and bearing long spines projecting from their posterior borders. Antopercular with curved posterior border. A single suborbital present. Maxilla bordering, or very close to, the ventral margin of the orbit. Teeth pointed and slightly recurved. Lower jaw deep posteriorly, tapering abruptly anteriorly. Lower jaw shorter than the upper jaw margin.

Body fusiform. Pectoral girdle ornamented with tubercles and parallel ridges. Scales rhombic and ornamented with tubercles. Jointing regular on all fin-rays, except the anterior rays of the pectoral fin which are unjointed. Fin-rays with large fulcra. Caudal fin hemiheterocercal and equilobate.

Type (and only) species. *Atopocephala watsoni* Brough.

Remarks. *Atopocephala,* although a member of the family Brookvaliidae, obviously represents a line which is separate from what may be regarded as typical members of the family—*Ischnolepis* and *Brookvalia.* The main feature of the genus is the shortness of the skull. As a result of this, the skull bones are relatively deeper than those of other brookvaliid genera, although the actual interrelationships of the bones remain unchanged.

Atopocephala watsoni Brough
(Fig. 7)

1934 *Atopocephala watsoni* Brough: 564–570, text-figs 2–3, pl. 1, figs 2–3.

Horizon and locality. Scythian. Lower Cynognathus zone of the Karroo Series at Bekker's Kraal, Rouxville, Orange Free State.

Diagnosis. As for the genus *Atopocephala.*

Holotype. P.16079–80. A specimen with counterpart, the only specimen known.

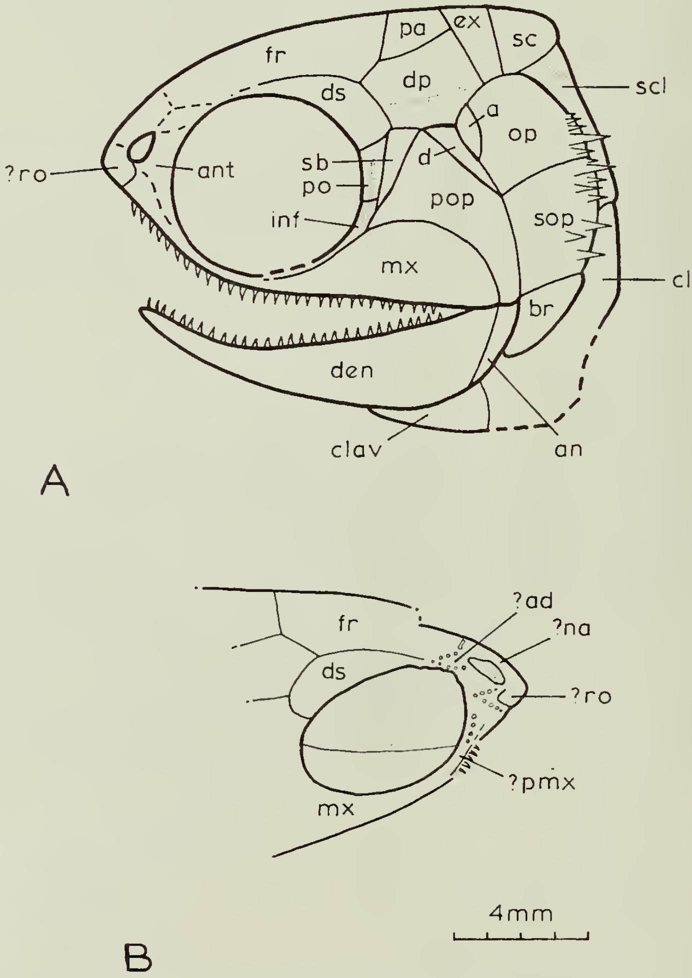

Fig. 7. *Atopocephala watsoni* Brough. (a) Restoration of skull and pectoral girdle, ×4·5 approx. (b) P.16080, impression of left side.

Description. The only additions to the description given by Brough (1934 : 564) are a new interpretation of the snout and of the opercular region (Fig. 7).

The snout region is difficult to interpret. The only certain features are the nostril outline, a suture running from the antero-ventral corner of the nostril to the edge of the snout and the presence of a toothed element on the ventral edge of the snout. The only other indications of the probable pattern of the bones of the snout consist of rows of tubercles. These are almost confluent, and form elongate rugae which may mark the outlines of elements (Fig. 7). The area occupied by the nasal in Brough's figure (1934 : text-fig. 3), contains two elements which are here interpreted as being the adnasal and antorbital. The anterior border of the orbit is formed by the antorbital. This element is separated from the ventral edge of the snout by a narrow (?) premaxilla. Dorsal to the top part of the antorbital there is a diamond-shaped adnasal which just borders the nostril anteriorly and the dermosphenotic posteriorly. The dorsal edge of the nostril is bordered by the nasal, a rectangular element which meets the frontal posteriorly and the rostral anteriorly. There is no postrostral.

Anterior to the opercular there is an antopercular and a dermohyal. The dermohyal is elongate and extends ventrally to the antero-ventral corner of the opercular. The antopercular has a curved posterior margin which fits into a notch in the antero-dorsal corner of the opercular (see Brough 1934 : pl. 1, fig. 3).

A suture between the angular and the dentary is clearly visible.

Genus ***BROOKVALIA*** Wade 1933

1933 *Brookvalia* Wade: 121
1935 *Brookvalia* Wade; Wade: 20
1935 *Dictyopleurichthys* Wade; Wade: 35
1935 *Beaconia* Wade; Wade: 33

Diagnosis (emended). Head bullet-shaped with large orbit anteriorly placed. Skull bones ornamented with tubercles. Posterior parietal triangular. Dermopterotic extensive dorsally and bearing a posterior extension of the supraorbital sensory canal. Frontal curved and elongate, bordering, or almost bordering, part of the dorsal edge of the orbit. Small rostral element at snout tip, probably bordering the anterior edge of the nostril. Opercular series narrow and moderately oblique. Maxilla bordering, or very close to, the ventral margin of the orbit. Teeth sharp, conical and numerous. Lower jaw with slight dorsal curve toward the symphysis. Lower jaw shorter than upper jaw margin.

Body fusiform. Pectoral girdle ornamented with parallel ridges. Scales leaf-shaped and ornamented with rugae. Jointing regular on all fin-rays except those of the pectoral fin, in which jointing only occurs distally on the anterior rays. Caudal fin hemiheterocercal and equilobate.

Type species. *Brookvalia gracilis* Wade.

Remarks. In this revision, five species classified in three genera by Wade (1935) have been reduced to four species, all included in a single genus. *B. parvisquamata* has been made a junior synonym of *B. gracilis* and *Dictyopleurichthys* *latipennis* has been included in the genus *Brookvalia*, but retains its identity at the species level because of its slightly different scale ornament. Finally, the identification of an antopercular and of a single branchiostegal in *Beaconia* makes the validity of that genus extremely doubtful, and the one species which it contained has been removed to the genus *Brookvalia*.

The members of *Brookvalia* as here constituted differ significantly from one another only in their overall body shape, in the shape of the caudal fin and in the size, shape and position of the dorsal fin.

Brookvalia gracilis Wade

(Figs 8–12, 14)

1933 *Brookvalia gracilis* Wade: 121–123, text-fig. 1.
1933 *Brookvalia parvisquamata* Wade: 124–125, text-fig. 3.
1935 *Brookvalia gracilis* Wade; Wade: 21–29, text-figs 5–14, pl. 4, fig. 1, pl. 5, fig. 1.
1935 *Brookvalia parvisquamata* Wade; Wade: 31–33, text-fig. 16, pl. 5, fig. 2.

HORIZON AND LOCALITY. Ladinian (?). 560 feet above the base of the Hawkesbury Sandstone, Beacon Hill, Brookvale, N.S.W.

DIAGNOSIS (emended). Extrascapular pentagonal. Two pairs of parietals, posterior element triangular, anterior element roughly oval and bearing two short parallel sensory canals. Dermopterotic bearing a short posterior extension of the supraorbital sensory canal. Postrostal probably present. Infraorbital elements reduced so that maxilla probably borders ventral edge of the orbit. Enlarged recurved teeth at tip of lower jaw.

Body slender. Scales ornamented with single, or rarely two, elongate rugae. Fringing fulcra not numerous, but present on anterior rays of all fins. Pectoral and pelvic fins equal in size, and fan-shaped with anterior and posterior rays almost equal in length. Dorsal fin originating just anterior to anal fin. Caudal fin deeply forked, with a few bifurcated rays in the lower lobe.

HOLOTYPE. P.15799 and counterpart P.15800.

MATERIAL. Holotype and P.15801–11, P.15813–24, P.15826–33, P.15835–42, P.15844–51, P.15853–6, P.15858, P.15860, P.15872, P.15878–9, P.15905–6, P.15914–5, P.15926, P.15930–1, P.15937, P.15939, P.15942, P.16997–17001, P.17005–17, P.24710–35.

U.S.G.D. 2, 4, 19, 28–9, 40–2, 80, 94, 141, 152, 159, 185–7, 205, 214, 218–19, 238, 244, 269, 272, 274, 277, 350 (at the University Museum of Zoology, Cambridge).

D.M.S.W. 383–8, 390–1 (at the University Museum of Zoology, Cambridge).

F.455 (at the Sedgwick Museum, Cambridge).

L.12143A–G.

DESCRIPTION. *Size* (Fig. 8). The total length from snout tip to the posterior end of the caudal fin varies from 30 mm (P.15810) to 125 mm (U.M.Z.C. uncatalogued). The body is fusiform and slender, its greatest depth occurring just behind the pectoral region.

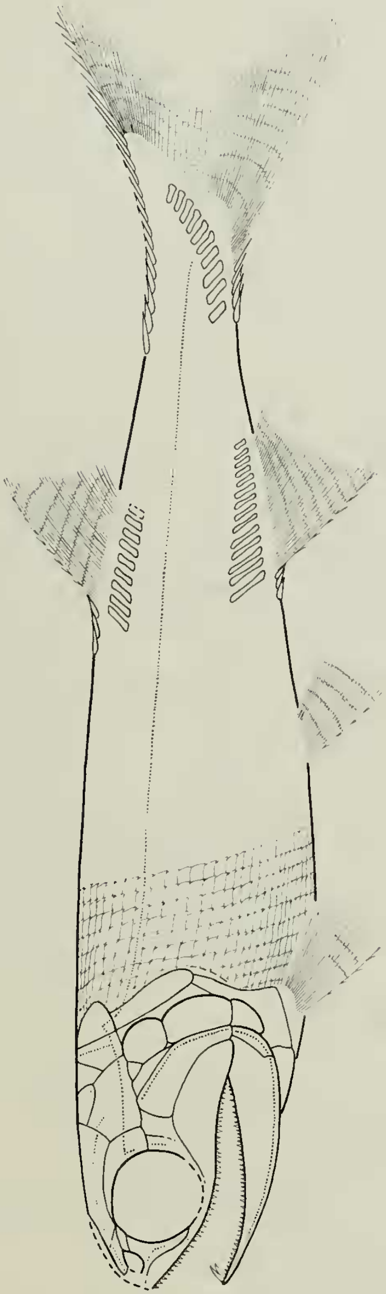

Fig. 8. *Brookvalia gracilis* Wade. Restoration, ×3 approx. Posterior scales omitted.

Skull (Fig. 9). The frontal is elongate, wide posteriorly and tapering towards the snout. It is sparsely covered with small tubercles. There are two pairs of parietals (parietal and postparietal of Wade). The anterior parietal is roughly oval, and bears three short rows of tubercles between which there were probably a pair of short sensory canals (U.S.G.D. 218 and P.15813, Fig. 10). The posterior parietal is larger than the anterior parietal and is triangular, coming to a point ventrally. In lateral aspect this element is small, but its dorsal extent is in fact quite large. It bears small tubercles. The dermopterotic is extensive, forming the main lateral element of the skull roof; it too bears tubercles.

The dermosphenotic is crescent-shaped and borders the postero-dorsal part of the orbit. Anteriorly it tapers to a point, but whether or not it meets the adnasal cannot be determined. It is thus possible that a small part of the frontal borders the dorsal edge of the orbit, though this is rather unlikely (see P.24730, Fig. 12).

In Wade's reconstruction of *B. gracilis* (1935 : text-fig. 5) the opercular lies ventral to the suprascapular and the extrascapular (post-temporal and tabular of Wade). This reconstruction is the result of misinterpretation of specimens in which opposite sides of the skull have been relatively displaced. In fact the opercular lies further anteriorly than in Wade's reconstruction with the result that the skull appears shorter, and the inferred angle of the suspensorium appears steeper (P.15813, Fig. 10). The opercular is oval and slightly longer than broad. It bears a series of low concentric ridges which follow the outline of the bone. The subopercular is elongate, being 1·5 times as deep as, and slightly longer than, the opercular. It

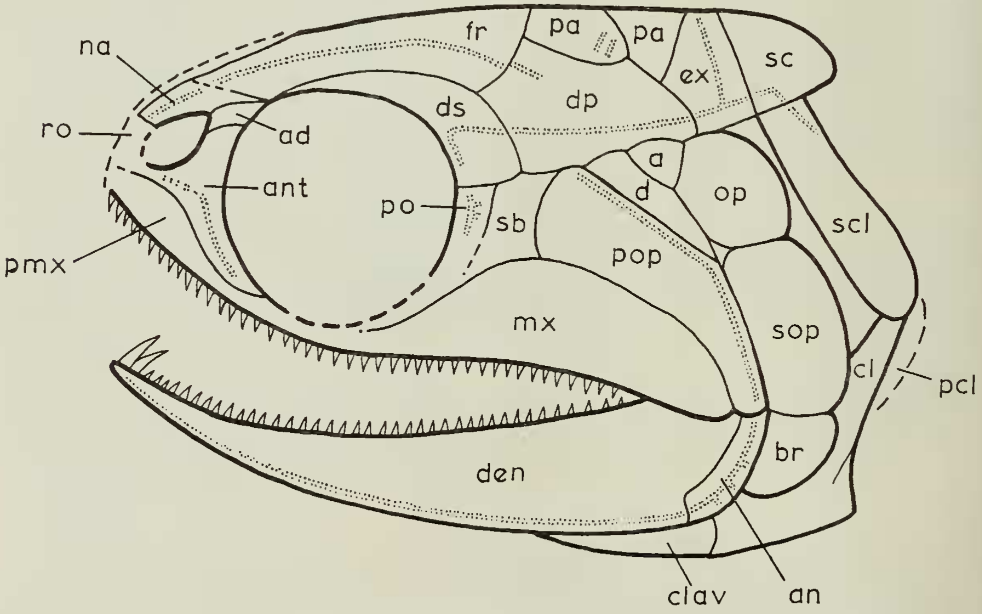

FIG. 9. *Brookvalia gracilis* Wade. Restoration of skull and pectoral girdle, ×5·5 approx.